THE EFFECTS OF LONG-TERM DROUGHT ON HOST PLANT CANOPY CONDITION AND SURVIVAL OF THE ENDANGERED *ASTRAGALUS JAEGERIANUS* (FABACEAE)

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Abstract

Astragalus jaegerianus Munz (the Lane Mountain milkvetch) is a federally endangered species that exists in only four fragmented populations within and adjacent to the U.S. Army's National Training Center, Fort Irwin, CA. Since 1999, our monitored *A. jaegerianus* populations have consistently declined, and are now 12% of their previous size. A number of subpopulations are in danger of local extinction. The decline of *A. jaegerianus* has occurred simultaneously with severe drought in the Mojave Desert. These drought conditions began in 1999 and are predicted to continue for decades, or may continue indefinitely under warmer temperature conditions projected by global climate change-type drought. Our results suggest that drought has direct and indirect affects on *A. jaegerianus* by killing or degrading its host shrubs. *Astragalus jaegerianus* host shrubs have decreased in shrub volume and cover by roughly 10 percent since the onset of drought, and shrub mortality has been high. Our results show that canopy condition has a profound affect on the microclimate within host shrubs. Furthermore, our results show a significant increase in survival of *A. jaegerianus* among host plants with more intact canopies. These results support our study hypothesis that drought-related changes to host plant canopies affect *A. jaegerianus* survival, and represent an indirect negative effect of long-term drought on *A. jaegerianus* populations.

Key Words: Endangered species, Lane Mountain milkvetch, Mojave Desert, plant-plant interactions, precipitation.

The Lane Mountain milkvetch, *Astragalus jaegerianus* Munz (Fabaceae), is a narrowly endemic plant that exists in small fragmented populations restricted to granite outcrops in the central Mojave Desert. Approximately two-thirds of all known *A. jaegerianus* populations occur within the boundaries of the U.S. Army's National Training Center at Fort Irwin, approximately 50 km NE of Barstow, CA (Charis Professional Services Corp. 2002). Because of its limited distribution and potential threat from military training, the U.S. Fish and Wildlife Service (USFWS 1998) listed *A. jaegerianus* as a federally endangered species in 1998.

A weak-stemmed herbaceous perennial, *A. jaegerianus* grows within the canopy of common desert shrubs such as *Thamnosma montana* Torr. & Frèm., *Ambrosia dumosa* (A. Gray) Payne, and *Eriogonum fasciculatum* Benth. The relationship between *A. jaegerianus* and its host shrubs is not clear. It is likely to be complicated because positive and negative effects of host plants on protégé occur simultaneously (Holmgren et al. 1997), and may change with host or protégé life stage (Shumway 2000; Miriti 2006; Reisman-Berman 2007). While adult *A. jaegerianus* are certainly dependent on host shrubs for structural support, host shrub canopies may provide *A. jaegerianus* with protection from herbivores (Gibson et al. 1998), as well as a modified

microclimate conducive to growth and recruitment of seedlings (Charis Professional Services Corp. 2002; Sharifi et al. 2009). Because of their proximity, *A. jaegerianus* and its host shrubs share water resources, but the degree to which they compete when water resources are limited is unknown. Although the relationship between *A. jaegerianus* and its host plants is likely to be antagonistic in some respects (e.g., competition for water or nutrients), in other respects host plants may benefit from the increased soil nitrogen associated with *A. jaegerianus* nitrogen fixation (Gibson et al. 1998).

For the past eleven years, this historically rare plant has undergone alarming population contractions. Since 1999, monitored *A. jaegerianus* populations have consistently declined, and in 2009 were less than 12% of their size in 1999 (Rundel et al. 2009). A number of subpopulations have dropped to critically low levels, and are in danger of local extinction (Rundel et al. 2009). This population decline has occurred simultaneously with recent severe drought conditions in the Mojave Desert (Hamerlynck and McAuliffe 2008) caused by regional climate patterns as well as global climate change processes (Hoerling and Kumar 2003). Drought in the Mojave began in 1999 and is predicted to continue for decades (Hereford et al. 2006), or may continue indefinitely under warmer temperature conditions

projected by global climate change-type drought (Cook et al. 2004; Breshears et al. 2005).

Drought conditions may have direct and indirect negative affects on *A. jaegerianus*. Laboratory studies suggest that frequent, above average winter precipitation is critical for seedling establishment and survival of *A. jaegerianus* (Rundel et al. 2005, 2006). These findings are supported by field studies that showed a small increase in *A. jaegerianus* seedling survival in 2005, an unusually wet year in the Mojave Desert. Drought conditions may also indirectly affect *A. jaegerianus*, by killing or degrading its host shrub. Recent drought conditions have led to unusually high shrub mortality and canopy dieback in the Mojave Desert and other parts of the arid southwest U.S. (Bowers 2005; Miriti et al. 2007; Hamerlynck and McAuliffe 2008; Hamerlynck and Huxman 2009). The deterioration of a host shrub's canopy due to drought should negatively affect *A. jaegerianus*, because shrub canopies provide shade, which affects the microclimate and water availability within and below shrubs (Valiente-Banuet et al. 1991; Nolasco et al. 1997; Shumway 2000; Flores et al. 2004; Barchuk et al. 2005) where *A. jaegerianus* carries out the majority of its early development as a seedling, and resprouts every year.

In this study we document the effects of severe long-term drought on the population dynamics of *A. jaegerianus*, evaluate the condition of *A. jaegerianus* host shrub canopies and their effect on sub-canopy microclimate, and investigate the effect of host shrub canopy condition on survival of *A. jaegerianus*.

METHODS

The *A. jaegerianus* populations monitored in this study are located in two adjacent geographic areas, the Gemini Conservation Area (GCA, previously referred to as Goldstone) and Brinkman Wash, previously established as discrete areas of *A. jaegerianus* distribution (Prigge et al. 2000; Charis Professional Services Corp. 2002; Walker and Metcalf 2008). Each area contains two study populations. The soils at these population sites are composed of shallow granite alluvium and rocky, granitic outcrops, within the transition zone between Mojavean creosote bush scrub and Joshua tree woodland communities.

Each *A. jaegerianus* study population is located on a 1 ha permanent plot that has either been surveyed since 1999 (Brinkman Wash) or 2003 (GCA). Each year several site visits are conducted to each of these permanent survey plots. During these visits, old, previously tagged plants and their host shrubs are located and searches are conducted for new plants under and around host shrubs and previously tagged *A. jaegerianus*

plants. Tagged *A. jaegerianus* plants are assessed to determine if they resprouted (alive) or not (dead or dormant). Seedlings found are measured for height and number of leaves and are revisited on subsequent surveys to monitor their development and survival. For all *A. jaegerianus* plants found, UTM coordinates are recorded using a GPS unit and readings from previous years are updated for accuracy.

During drought, living shrubs may shed foliage as a result of water stress, and to reduce carbon allocation and increase water-use efficiency (Hereford et al. 2006). This process creates defoliated gaps in shrub canopies, reducing their capacity to shade sub-canopy microhabitats. In 2009, the dimensions of host shrubs with live or dead *A. jaegerianus* were recorded, and the foliation level of each *A. jaegerianus* host shrub canopy was estimated as a percentage of its total canopy minus dead, defoliated canopy.

In addition to host shrub measurements made during *A. jaegerianus* surveys, shrubs were resurveyed along vegetation transects established in 2000 (Prigge et al. 2000). These shrub transects were located within high-density *A. jaegerianus* populations, but no *A. jaegerianus* occurred within the transects. Measurement of shrub density, frequency, and cover was done by using 2 belt-transects (Mueller-Dombois and Ellenberg 1974). Transects were 24 m long and 2 m wide. Cover was determined by measuring the maximum diameter (d_1) and the diameter (d_2) perpendicular to the maximum and calculating the area for an ellipse (cover = $[d_1/2][d_2/2]\pi$). Shrub volume was determined using an additional height (h) measurement and calculating the volume of an ellipsoid (volume = $4/3\pi d_1 d_2 h$).

To determine the effect of canopy condition on the microclimate within host shrubs, three shrubs with canopies and three recently dead shrubs without leaves but with branches intact were selected for measurement. Light intensity (PFD) was measured using a solar monitor (Licor L1-1776) attached to a quantum sensor (Licor L1-190SB) placed in a horizontal position close to the interior base of the host shrub. Soil surface temperature was measured using a thermometer (Omega HH21) attached to thermocouples placed no more than 1 mm beneath the soil surface at the base of the shrub. Temperature and light measurement were taken on the hour from 6:00 a.m. to 8:00 p.m.

Precipitation data were obtained from the remote automated weather station at Opal Mountain CA (35°09′15″E; 117°10′32″W; 988 m). This weather station is approximately 30 km from monitored Milkvetch sites at a similar elevation. The Opal Mountain data were in near perfect agreement with data collected closer to *A. jaegerianus* populations (Rundel et al. 2006), but has the advantage of being continuous
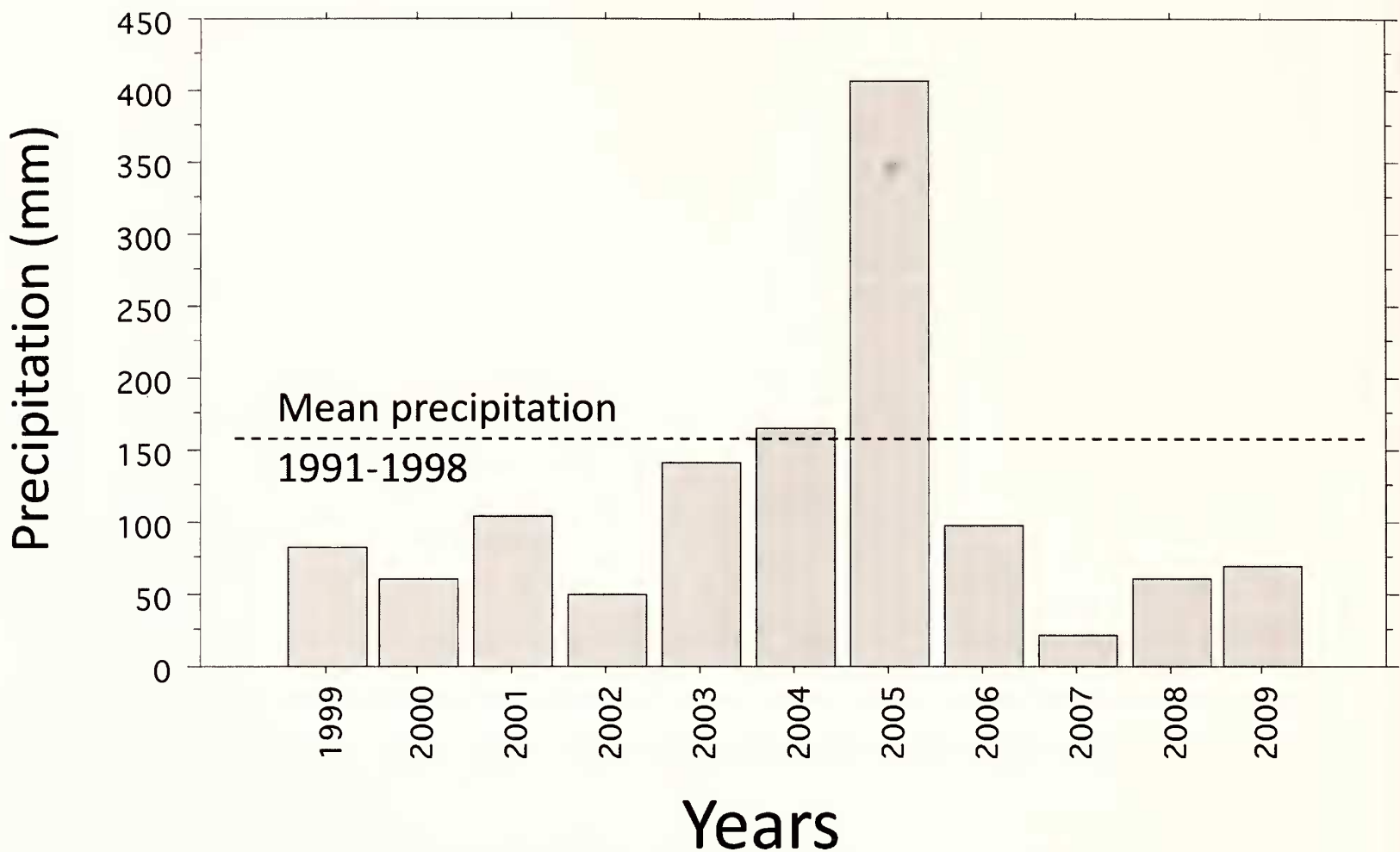
Fig. 1. Annual precipitation (OCT-SEP) from 1999 to 2009 at the remote automated weather station at Opel Mountain, CA (35°09′15″E; 117°10′32″W; 3240 ft). Years refer to the season in which *Astragalus jaegerianus* is reproductive (for example, 1999/2000 is denoted as 2000). This weather station is approximately 18 mi from monitored *A. jaegerianus* sites and at a similar elevation. The dash line is mean precipitation (160.4 mm·yr⁻¹) from 1991 to 1998 at the same location. The mean precipitation during the current drought from 1999 to 2009 was 114.4 mm·yr⁻¹. Weather data archived by the Western Regional Climate Center.

from 1992 to the present. Precipitation from October through September was used because it includes winter and spring rainfall that affects *A. jaegerianus* growth and reproduction. Thus, annual precipitation includes October through December precipitation of the previous year.

Shrub data were analyzed using Statview (SAS Institute Inc., Cary, NC). Nonparametric statistics were used because some shrub data was not normally distributed and resistant to transformation to normality (SAS 1999). Paired sign tests were used to analyze changes in shrub volume and cover. An unpaired t-test was used to compare shrub canopy condition in shrubs that supported live *A. jaegerianus* with shrubs in which *A. jaegerianus* had died since monitoring began in 1999 (Brinkman Wash) and 2003 (GCA).

RESULTS

The current drought began in the fall of 1998 (Hereford et al. 2006) and is in its eleventh year (Fig. 1). Despite an unusually wet 2005 (407 mm), this drought period has a mean precipitation of 114.4 mm·yr⁻¹ compared to the relatively wet years preceding it from 1991 to 1998, in which mean precipitation was 160.4 mm·yr⁻¹. These wet years represent the tail end of a wet period from 1976 to 1998 (Hereford et al. 2006) that presumably generated the high *A. jaegerianus* population numbers recorded in 1999. While the difference in precipitation between these wet and dry periods is considerable (46.1 mm·yr⁻¹), the severity of the drought and its impact on *A. jaegerianus* is better appreciated by considering the years before and after 2005; the six-year period between 1999 and 2004 had a mean precipitation of 100.5 mm·yr⁻¹, and the four year period from 2006 to the 2009 had a mean precipitation of 61.9 mm·yr⁻¹. The year 2007 had the lowest precipitation in the 1991 to 2009 Opel Mountain data set (22 mm).

While *A. jaegerianus* continues to decrease in density at our long-term study sites, its decline has slowed and appears to be reaching a plateau (Fig. 2). No *A. jaegerianus* mortality was observed in Brinkman Wash populations in 2009, and GCA populations lost only two *A. jaegerianus*, the lowest absolute decline in seven years of observation. Despite these decreases in mortality, *A. jaegerianus* numbers remain dangerously low. Of the 161 original plants at the four study sites, only 20 remain alive, with zero recruitment of new *A. jaegerianus* plants and 100% seedling mortality since surveys began in 1999 (Brinkman
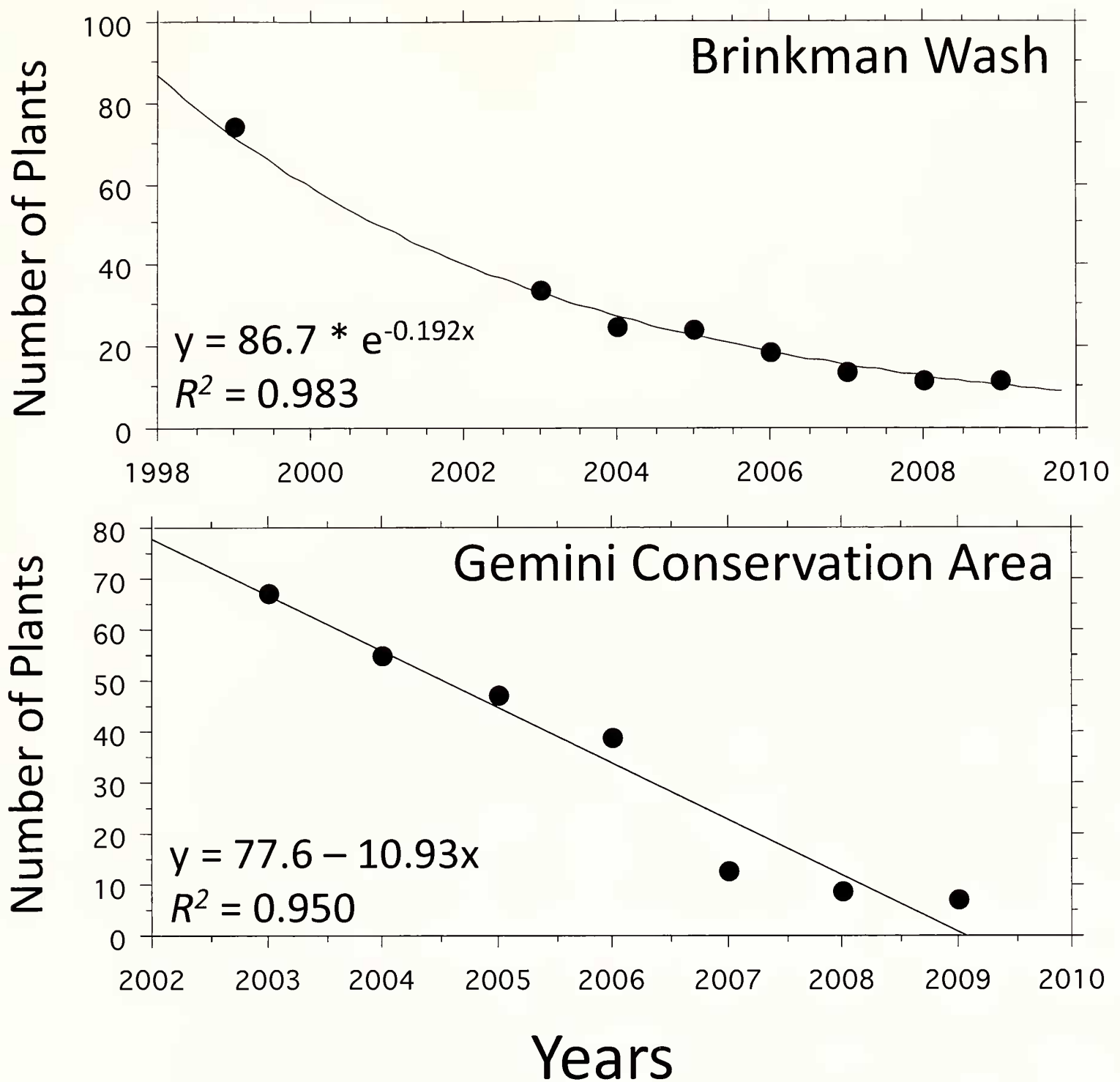
FIG. 2.   Population declines of *Astragalus jaegerianus* at two study areas, Brinkman Wash (1999, 2003 through 2009) and Gemini Conservation Area (2003 through 2009). Each study area contains multiple monitored *A. jaegerianus* populations.

Wash) and 2003 (GCA). All monitored populations have dropped to critical levels and are at risk of local extinction. Assuming that the *A. jaegerianus* mortality observed at our long-term study sites is characteristic of the species across its range, the 5723 mature *A. jaegerianus* plants which constituted the plants found in 2001 (Charis Professional Services Corp. 2002) would now number approximately 686 individuals.

One of these populations precariously close to extinction is M2 at Brinkman Wash (Fig. 3). Since 1999, M2 has declined from 23 plants to one remaining plant. However, mortality has not been constant; population decreases were relatively slow between 1999 and 2003, but accelerated between 2003 and 2006 to a loss of 6 plants per year in 2005 and 2006 (Fig. 3). Although 2005 was an unusually wet year with more than

twice mean annual precipitation, it appears that even this unusually high rainfall could not diminish the momentum of *A. jaegerianus* mortality. By 2007, population M2 had fallen to one plant that has managed to survive the last three years of intense drought.

Host shrubs populations have declined simultaneously with the decline of *A. jaegerianus* populations. In our shrub transects within *A. jaegerianus* sites, while some shrubs increased in size, total shrub cover and volume have decreased significantly by roughly 10% between 2000 and 2009 (Fig. 4; paired sign test: $P < 0.001$, $n = 75$, for both shrub cover and volume). Mortality of these long-lived shrubs has been high (48%), and the recruitment of new shrubs (5%) has been too low to maintain their populations at previous levels. Among *A. jaegerianus* host shrubs, shrubs
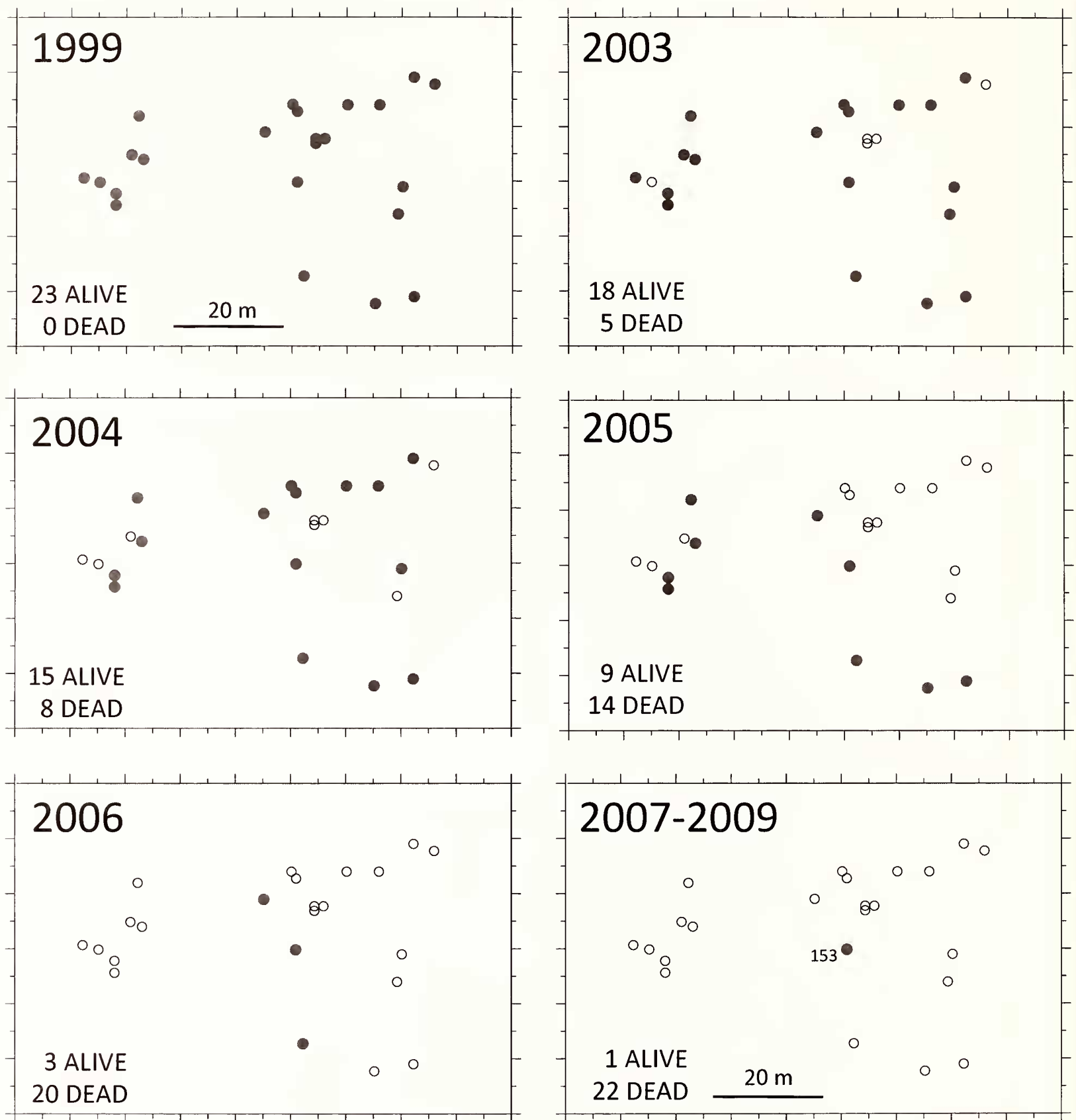
FIG. 3. Aerial view of *Astragalus jaegerianus* population M2 at the Montana Mine site (1999, 2003, 2004, 2005, 2006, 2009). Solid dots are live *A. jaegerianus* plants, and empty dots are dead *A. jaegerianus*. Population M2 decreased from 23 *A. jaegerianus* plants in 1999 to one plant in 2009. No recruitment has been observed at this site during this period. The position of *A. jaegerianus* plants was determined using each plant's UTM coordinates.

with live *A. jaegerianus* have more intact canopies than host shrubs that once supported *A. jaegerianus*, which are now dead (Fig. 5; unpaired t-test: $F_{1,118} = 11.48$; $P = 0.0010$).

Soil surface temperature and light intensity beneath shrubs were dependent on the condition of the shrub's canopy; shrubs with open canopies had light levels five times higher than shrubs with closed canopies, and soil surface temperature beneath shrubs with open canopies were as much as 20°C higher than shrubs with closed canopies

(Fig. 6). While most shrubs do not have completely open canopies, among LMMV host shrubs originally surveyed in 1999 and 2003, the average host shrub had only 45 percent of its canopy intact in 2009.

DISCUSSION

Studies in arid and semi-arid environments demonstrate that the shade produced by host plant canopies mitigate severe abiotic conditions
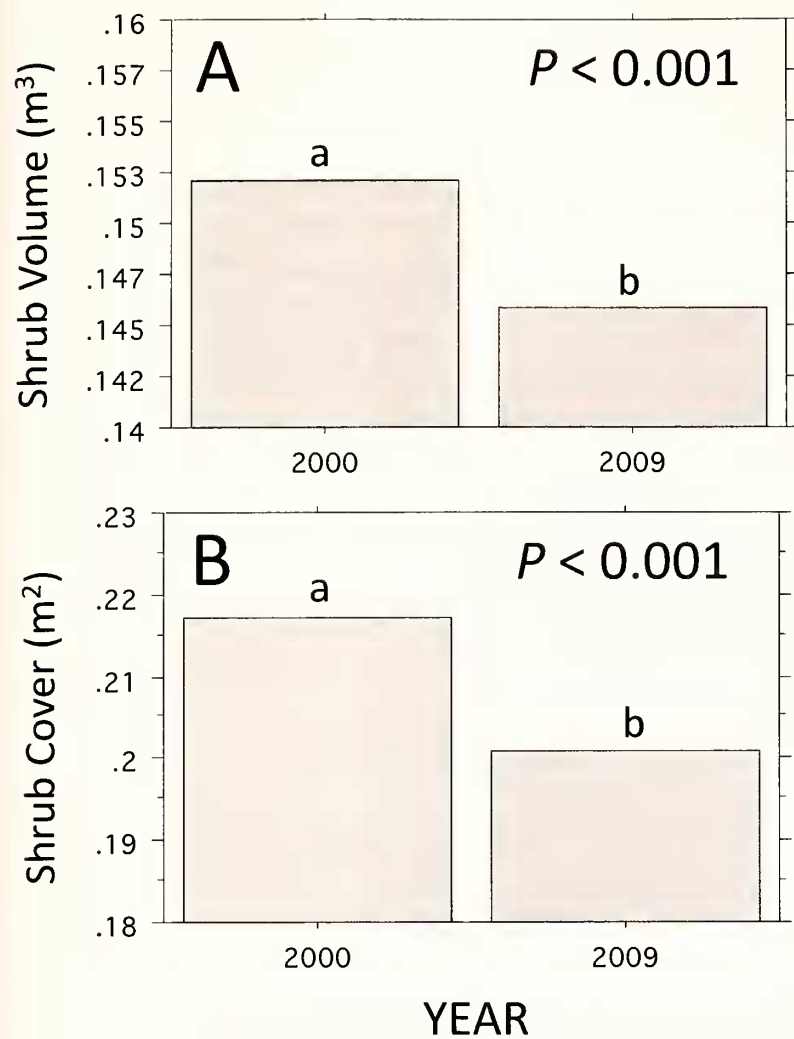
FIG. 4. Changes in shrub size between 2000 and 2009. Both shrub volume and shrub cover deceased significantly in the nine years between censuses. Shrubs were censused along a transect adjacent to *A. jaegerianus* population M1. A. Mean shrub cover measured as an ellipsoid (paired sign test: P < 0.001, n = 75). B. Mean shrub cover measured as an ellipse (paired sign test: P < 0.001, n = 75).
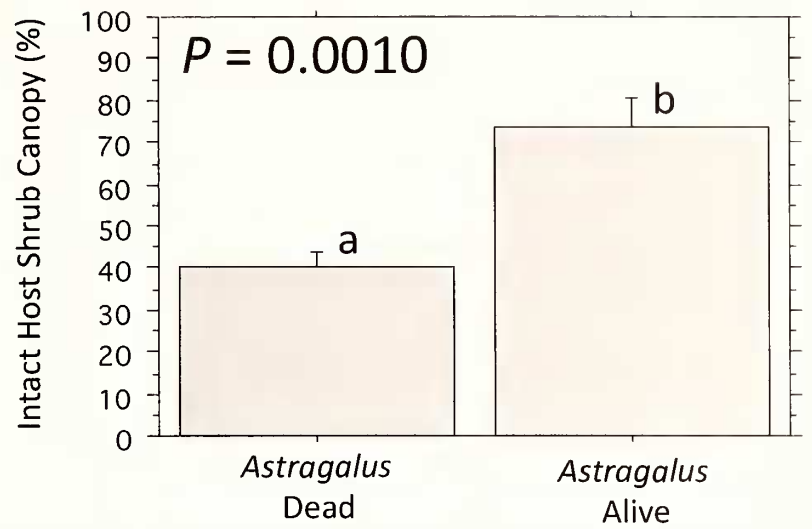

FIG. 5. Percent live host plant canopy and *Astragalus jaegerianus* status, GCA and Brinkman Wash site combined, 2009. *Astragalus jaegerianus* was found in host shrubs with more intact canopies (unpaired t-test: $F_{1,118} = 11.48$; P = 0.0010). Intact host shrub canopy condition was estimated as a percentage of total canopy (live plus dead canopy).

by reducing air and soil temperature (Franco and Nobel 1989; Valient-Banuet et al. 1991; Paez and Marco 2000; Flores et al. 2004), and increasing soil moisture availability (Nolasco et al. 1997; Shumway 2000; Warnock et al. 2007). Facilitation occurs when microclimate effects such as these increase the establishment and survival of protégé plants growing under host shrub canopies (Cody 1993). Because the facilitative effect of host plants depends on the capacity of its canopy to modify the environment beneath it, changes in canopy structure can affect the facilitative effect of the host plant (Reisman-Berman 2007).

In this study we have documented the drought-induced mortality and canopy deterioration of *A. jaegerianus* host plants, and have demonstrated the effect of host plant canopy foliation on soil temperature and light intensity in sub-canopy, *A. jaegerianus* microhabitat. We have also demonstrated a significant increase in survival of *A. jaegerianus* among host plants with more intact canopies. These results support our study hypothesis that drought-related changes to host plant canopies affect *A. jaegerianus* survival, and represent an indirect negative effect of long-term
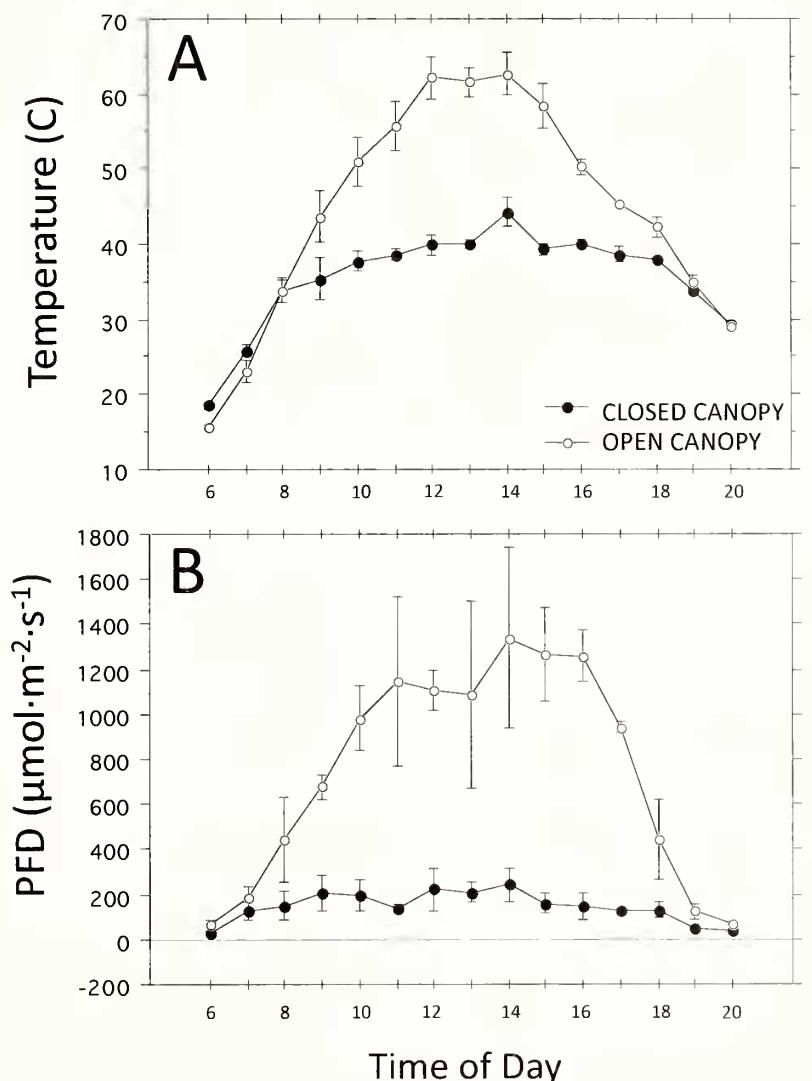

FIG. 6. The effect of *Astragalus jaegerianus* host shrub canopy condition on shrub micro-climate in June 2009 at *A. jaegerianus* population M1, Montana Mine site, Brinkman Wash. A. Soil surface temperature beneath open and closed canopy shrubs (6:00 to 20:00). B. Light intensity (photon flux density, $\mu mol \cdot m^{-2} \cdot s^{-1}$) beneath open and closed canopy shrubs (6:00 to 20:00). Closed circles are measurements recorded under shrubs with closed canopies. Open circles are values recorded under shrubs with open canopies. Points are means with standard errors (n = 3).

drought on *A. jaegerianus* populations. Theory suggests that positive and negative interactions should change along gradients in abiotic stress, with positive interactions dominating under harsh physical conditions where host plants ameliorate abiotic stress (Bertness and Callaway 1994). While a number of studies have demonstrated the positive, facilitative effect of host plants in stressful arid environments (Valiente-Banuet and Ezcurra 1991; Paez and Marco 2000; Pugnaire and Luque 2001; Barchuk et al. 2005; Miriti 2006; Reisman-Berman 2007), to our knowledge, the idea that severe stress associated with long-term drought may diminish host plant facilitation through negative effects on host plant canopies has not been previously documented.

The negative effects of long-term drought on Sonoran, Great Basin, and Mojave Desert perennial plants are well documented (Goldberg and Turner 1986; Turner 1990; Bowers 2005; Hereford et al. 2006; Miriti 2006; Hamerlynck and McAuliffe 2008; Hamerlynck and Huxman 2009; Ralphs and Banks 2009), and are similar to drought effects described in this study for *A. jaegerianus* host shrubs: high shrub mortality, shrub canopy deterioration, and low recruitment. Increases and decreases in mortality associated with fluctuation in interannual precipitation have been reported in other herbaceous desert perennials (*Cryptantha flava* (A. Nelson) Payson, Casper 1996), and the population declines of *A. jaegerianus* fit this general pattern, with the exception of 2005, when adult *A. jaegerianus* mortality continued more or less unaffected by unusually high precipitation (e.g., M2 at Brinkman Wash experienced its highest recorded adult mortality in 2005 and 2006). Seedling establishment also responded weakly to the increase in precipitation in 2005; nine seedlings were established, went dormant through the summer of 2005, and resprouted in 2006. While this was the only observed case of seedling establishment since 1999, 2006 was again a drought year, and these resprouted, second-season plants did not achieve reproductive maturity, and failed to resprout in 2007.

The reason for this insensitivity to increased precipitation in 2005 is unclear, but could be the result of the accumulated damage to host shrub canopies inflicted by long-term drought. The effects of drought on *A. jaegerianus* host plants may proceed rapidly because of positive feedback within the canopy/micro-climate interaction; as shrub canopies deteriorate, evapotranspiration beneath shrubs increases, which increases shrub water stress leading to further canopy deterioration. This positive feedback between shrub canopy and microclimate, and the slow growing nature of desert shrubs may explain why the momentum of *A. jaegerianus* population declines could not be slowed by a single year of high rainfall in 2005.

Episodic recruitment associated with high precipitation has been observed or inferred from demographic analysis in a number of desert perennials (Shreve 1917; Barbour 1969; Sheps 1973; Jordan and Nobel 1979, 1982; Goldberg and Turner 1986; Turner 1990; Parker 1993; Bowers 1995; McDaniel et al. 2000; Godinez-Alvarez et al. 2003). We have previously hypothesized that pulses in high annual precipitation, such as those associated with ENSO events, drive *A. jaegerianus* recruitment, and between high recruitment years mortality occurs in a more or less constant manor (Sharifi et al. 2009). Consistent with this pulse model is the expectation that *A. jaegerianus* recruitment and mortality should be sensitive to years with high rainfall, and recruitment should increase during high rainfall years; but continued adult mortality and low recruitment through an unusually wet year like 2005 suggests that *A. jaegerianus* recruitment is likely to be gradual, and may occur during long-term wet periods. Long-term wet periods in the Mojave Desert occur more or less regularly, and are associated with the Pacific Decadal Oscillation that causes decadal-scale variability such as prolonged dry and wet episodes (Hereford et al. 2006). Prolonged wet periods in the Mojave Desert, such as 23 yr wet period between 1976 and 1998, may positively affect *A. jaegerianus* population growth factors that are relatively insensitive to short-term precipitation such as the condition of slow-growing host shrub canopies. Similarly, dry periods result in the deterioration of host plant canopies, which diminishes *A. jaegerianus* recruitment even during years of high precipitation such as 2005. An expectation of this climate-period model is that the sensitivity of recruitment to precipitation is dependent on the climatic context in which precipitation occurs: recruitment sensitivity is high during prolonged wet periods and low during dry periods. Given these hypothetical circumstances, *A. jaegerianus* populations would tend to oscillate between multi-decadal, high and low population states that are determined by long-term precipitation patterns characteristic of climate-periods.

Although adult *A. jaegerianus* mortality has occurred each year since observations began in 1999, mortality has slowed and stopped in some populations. In population M2 (Fig. 3), a single remaining LMMV has survived alone for three years despite the intense drought (mean precipitation 50 mm·yr^{-1}, 2007–2009, Fig. 1). *Astragalus jaegerianus* it thought to be deep-rooted, and this drought-resistant plant may have access to deeper or more reliable sources of water in its fractured granite substrate, and thus better water relations, than *A. jaegerianus* that died earlier in the drought. This idea assumes that soil water resources are heterogeneous, and that only the most consistent water resources are able to

maintain *A. jaegerianus* after prolonged drought. Reduced but persistent populations of *A. jaegerianus* are consistent with expectations of the climate-period model described above.

Our previous studies have shown that *A. jaegerianus* seed density is low to extremely low in the soil seed band compared to other desert shrubs (Rundel et al. 2009; Rundel and Gibson 1996), and seed dispersal beyond host shrub canopies is rare (Rundel et al. 2009). For *A. jaegerianus*, these are grim ecological circumstances: as its host shrubs deteriorate and die, and without the ability to disperse to other host shrubs, its recovery to 1999 populations levels in the immediate future is unlikely. If our climate-period model is correct, and surviving, drought resistant *A. jaegerianus* have access to deep, reliable water sources, drought-reduced populations could persist until the current drought is over, and then expand under wetter climatic conditions. However, if drought conditions continue, it is equally possible that *A. jaegerianus* numbers may erode further, leaving most, if not all populations in eminent danger of local extinction. Unfortunately, regional climate indicators suggest that the Mojave Desert may remain dry for 1 to 2 decades or longer (Breshears et al. 2005; Hereford et al. 2006). In anticipation of prolonged drought, efforts should be made to preserve the *A. jaegerianus* as a unique and rare component of the Mojave Desert flora. These efforts should focus on habitat preservation, experimental repopulation of endangered or extinct subpopulations, and further investigation into the effects of drought on facilitative interactions between *A. jaegerianus* and its host shrubs.

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